

## Influence of Size-Selective Mortality on Growth of Gulf Menhaden and King Mackerel Larvae

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**Abstract.**—Gulf menhaden *Brevoortia patronus* and king mackerel *Scomberomorus cavalla* represent two widely different larval life history strategies: feeding on large and small prey, respectively. We back-calculated lengths at age for wild and laboratory-reared larvae of gulf menhaden and wild king mackerel using direct proportion procedures then constructed matrices of observed age (rows) by increment number (columns) for mean back-calculated lengths at age. The coefficient of variation (100·SD/mean) in length at age was greater for observed than for back-calculated length at age for both wild and laboratory-reared gulf menhaden and for king mackerel. Columns in the length-at-age matrix of wild gulf menhaden showed significant trends of increasing back-calculated length at age for older larvae, but the matrix for laboratory-reared fish did not. We suggest that size-selective mortality—the culling of slower-growing larvae—was the cause of the different error structures of observed and back-calculated lengths at age as well as of the increasing back-calculated lengths at age for older larvae in the matrix of wild gulf menhaden. Predation may have been the cause of size-selective mortality because wild larvae were exposed to predation and laboratory-reared larvae were not. Slopes of regressions of back-calculated length on observed age for columns of the matrices indicate the time trend and intensity of size-selective mortality; in wild gulf menhaden larvae, size-selective mortality began after hatching, reached a plateau at 5–8 d, then declined markedly after 14 d, which suggests that the influence of predation was mainly expressed during this period. Size-selective mortality caused average growth (mean back-calculated or observed length at age) to appear higher for both species, but especially for gulf menhaden, because the smallest larvae of a given age were removed. We adjusted back-calculated growth by removing the effect of size-selective mortality with analysis of covariance and estimated that the observed growth rate was 25% higher than the adjusted rate for wild gulf menhaden and 7% higher for wild king mackerel.

Pannella (1971) first documented the existence of daily growth increments on fish otoliths over 20 years ago, and the presence of daily increments has now been verified in many species (Jones 1986). Although many scientists have extracted daily age-and-growth information since the development of the procedure, the technique has not been fully exploited to extract information on the dynamics of larval growth and mortality. A strong relationship between otolith size and fish size is necessary to determine the size of an individual larva at each day of life by back-calculation techniques (Campana and Neilson 1985; Mosegaard et al. 1988). Some studies have suggested that on a day-to-day basis, otolith increment width and fish growth can be decoupled under some circumstances (Volk et al. 1984; Neilson and Geen 1985; Bradford and Geen 1987; Gutierrez and Morales-Nin 1986; Malony and Choat 1990; Secor and Dean

1989). But when otolith size and fish size are strongly related, back-calculation provides a good estimate of the growth trajectory of individual larvae (Methot 1981; Penny and Evans 1985; Savoy and Crecco 1987; DeVries et al. 1990; Jenkins and Davis 1990; Thorold and Williams 1989).

The subject of size-dependent mortality has received considerable attention in studies of larval fish ecology. That larger and faster-growing fish larvae are more likely to survive is widely accepted (Peterson and Wroblewski 1984; McGurk 1986; Houde 1987; Anderson 1988; Miller et al. 1988; Pepin 1988, 1989, 1991; Beyer 1989; Bailey and Houde 1989), although this view has been challenged (Litvak and Leggett 1992; Pepin et al. 1992). Both predation and starvation are size dependent (Rosenburg and Haugen 1982; Pepin et al. 1987). Small fish larvae are most vulnerable to starvation (Beyer and Laurence 1980; Rosenburg and Haugen 1982; Margulies 1993); vulnerability to predation depends upon larval size and growth rate (Shepherd and Cushing 1980; Bailey 1984; Bailey and Batty 1983; Purcell 1986), the relative

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size of predators (Gerritsen and Strickler 1977; Pepin et al. 1987; Cowan and Houde 1992; Pepin et al. 1992), and the densities and capabilities of both predators and larval fish prey (Cowan and Houde 1992).

Although back-calculated length-at-age data can be useful in evaluating survival and mortality trends, they have only occasionally been used for young fishes to this end. Post and Prankevicius (1987) compared daily back-calculated lengths to observed lengths of yellow perch *Perca flavescens* for specific dates and found that observed lengths at age were less than back-calculated ones. They concluded that the differences in back-calculated and observed lengths probably resulted from size-selective mortality. Similarly, Barkman and Bengston (1987) used weekly increment widths measured from five fish collected at the end of the growth season to back-calculate an absolute growth curve for the Atlantic silverside *Menidia menidia*. Back-calculated growth was not significantly different from observed growth, indicating that no size-selective mortality occurred. Al-Hossaini et al. (1989) measured seven consecutive radii on otoliths of plaice *Pleuronectes platessa* and compared back-calculated length at age to observed length at age. Fitted curves for observed and back-calculated growth were significantly different (observed growth was greater), which suggests that the differences might be attributed to size-selective mortality. Healey (1982) demonstrated size-selective mortality from back-calculated length distributions from spacing of scale circuli. Fitzhugh and Rice (1995) evaluated the error in back-calculation of length at age from otoliths of southern flounder *Paralichthys lethostigma* and discussed the implications for analysis of size-dependent processes.

Using back-calculation, we evaluated the potential influence of size-selective mortality on growth rate, tested predation as the possible cause of size-selective mortality, and quantified the impact of size-selective mortality on growth rate. We produced half-rank matrices of mean back-calculated lengths at age for wild and laboratory-reared larval gulf menhaden *Brevoortia patronus* (reasoning that wild larvae had experienced predation, whereas laboratory-reared larvae had not) and wild larval king mackerel *Scomberomorus cavalla*. The matrix is analogous to annual length-at-age matrices of identical form that have been common in the fishery literature for over 50 years (e.g., see Ricker 1975:220). We chose king mackerel, a scombrid, and gulf menhaden, a clupeid, because

they represent different larval life history strategies: feeding on large and small prey, respectively (Hunter 1981). King mackerel feed on other fish larvae almost exclusively (Finucane et al. 1990); menhaden feed on small phytoplankton and zooplankton (Govoni et al. 1983). Feeding on larger prey requires a large mouth and greater, more efficient effort because food density declines exponentially with food size in the sea (Vlymen 1977). Persistence in attack, maneuverability, and greater searching effort, also necessary for the large-prey strategy, require a faster swimming speed and a higher metabolic rate and greater energy requirements. The faster swimming speed results in lower vulnerability to predation but higher encounter rates (Bailey and Houde 1989). The higher metabolic rate and energy requirements promote more rapid growth in the presence of adequate food, which reduces the duration of the larval stage, the period of greatest vulnerability to predation, thus reducing the total impact of predation. King mackerel larvae grow rapidly (0.8 mm/d, DeVries et al. 1990); whereas the growth of gulf menhaden larvae is more modest (0.3 mm/d, Warlen 1988).

### Methods

King mackerel larvae were collected from the Gulf of Mexico on 3–26 September 1986 with 1 × 2-m neuston nets (0.947-mm mesh) and 60-cm bongo nets (0.333-mm mesh). Upon capture, fish were preserved in 95% ethanol for 24 h, after which the preservative was drained and fresh ethanol was added. Wild gulf menhaden were collected off Southwest Pass in the vicinity of the Mississippi River discharge plume during December and February of 1979–1982 with a 1.0-m<sup>2</sup> (effective sampling area) multiple opening-closing net and environmental sensing system (MOCNESS: Wiebe et al. 1976), and 60-cm bongo nets fitted with 0.505-mm mesh nets. We obtained laboratory-reared gulf menhaden larvae that were hatched and reared at the National Marine Fisheries Service laboratory in Beaufort, North Carolina (Warlen 1988), from eggs obtained from adults collected from the Gulf of Mexico off Gulf Breeze, Florida (Hettler 1983). Larvae were fed rotifers at a concentration of 25 prey/mL. Some larvae were removed on days 7, 10, 14, 17, 20, 24, and 31 posthatch and preserved in 95% ethanol.

We measured each larva to the nearest 0.1 mm standard length (SL) with an ocular micrometer. Because all of our samples were immediately pre-

served in ethanol, we concluded that it was reasonable to ignore shrinkage effects when evaluating growth and size-dependent mortality rates (Radtke 1989). Using a dissecting microscope (12–50 $\times$ ), we removed sagittal otoliths from the heads of larvae, washed them with distilled water, and dried and mounted them on glass slides under a thin layer of FLO-TEXX,<sup>2</sup> a polymer mounting medium. Polishing the otoliths was not required for increment analysis because they were thin enough that focusing to the plane of maximum clarity was sufficient to obtain total ring counts and measurements (Brothers et al. 1976).

Whole otoliths were examined under transmitted light at 400 $\times$  magnification with a compound microscope video image analysis system. This system was used to measure otolith radii in the antistrostral region of the otolith. We jointly identified growth increments and made radius measurements.

The back-calculation procedure consisted of three steps. First, we measured the distances (0.001 mm) from otolith primordia to successive growth rings and to the otolith margins (radius). Second, we computed the regression of SL (0.1 mm) on otolith radius separately for wild and laboratory-reared gulf menhaden and wild king mackerel and used the regression intercepts as correction factors to back-calculate fish length at each growth ring according to the Fraser–Lee direct proportion method (Carlander 1981). This is similar to the biological intercept method recommended by Campana (1990). Fitzhugh and Rice (1995) used linear and multiple regression procedures as well as the biological intercept and Fraser–Lee methods for back-calculating length at age for southern flounder juveniles; linear regression yielded the lowest error, but Fitzhugh and Rice cautioned that this might have been a special case. Last, the estimates of back-calculated lengths at age were used to construct increment (ring) number by observed-age half-rank matrices of mean back-calculated lengths at age (e.g., Table 1).

We used analysis of covariance (ANCOVA) to test for significant evidence of size-selective mortality in back-calculated length-at-age matrices of wild and laboratory-reared larvae. Models evaluated differences in back-calculated lengths at age while controlling for differences with increasing increment number (row effects). We also used AN-

COVA to evaluate growth differences between wild and laboratory-reared gulf menhaden larvae.

To quantify the effects of possible size-selective mortality on growth, we calculated regression coefficients for the relationship between back-calculated length at age and observed age for each increment number (column) in the matrix. The slopes of these regressions are estimates of the intensity of size-selective mortality, as well as the bias in growth resulting from size-selective mortality. We used ANCOVA to estimate the magnitude of the influence of size-selective mortality and to correct growth (regressions of observed and back-calculated length on age) for the effects of size-selective mortality by adding observed age (column effects) as a covariate to the growth model.

## Results

The sagittae of both gulf menhaden and king mackerel have clearly visible growth increments, allowing us to easily measure distances from primordia to the outer edge of each increment, consisting of a pair of light (opaque) and dark (translucent) rings, and to the otolith margin (radii) (Figure 1). These growth increments are deposited daily in otoliths of larval gulf menhaden (Warlen 1988) and king mackerel (DeVries et al. 1990) and are useful for describing growth rates. We measured otolith radii on otoliths of 92 gulf menhaden larvae (47 from the wild and 45 reared in the laboratory), which ranged from 5.4 to 18.1 mm SL (wild, 5.4–18.1 mm; laboratory-reared, 6.4–17.2 mm) and 51 king mackerel larvae, which ranged from 3 to 11 mm SL. Ages ranged from 5 to 33 d for gulf menhaden and from 2 to 11 d for king mackerel.

In gulf menhaden sagittae, all growth increments were clearly recognizable. After preliminary examination of the king mackerel otoliths, we observed that one and sometimes two faint increments near the primordium were followed by a consistently observable ring. Because the faint rings were difficult to distinguish, we decided to begin increment counts at the first clearly visible ring, which we designated as the second ring. Subsequent increment measurements were made from the primordium to the second ring and to all successive rings.

We computed regressions of SL on total otolith radius for both species (Figure 2). The relationships for laboratory-reared and wild gulf menhaden and king mackerel were linear within the range of observed lengths of larvae. The intercepts of

<sup>2</sup> Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

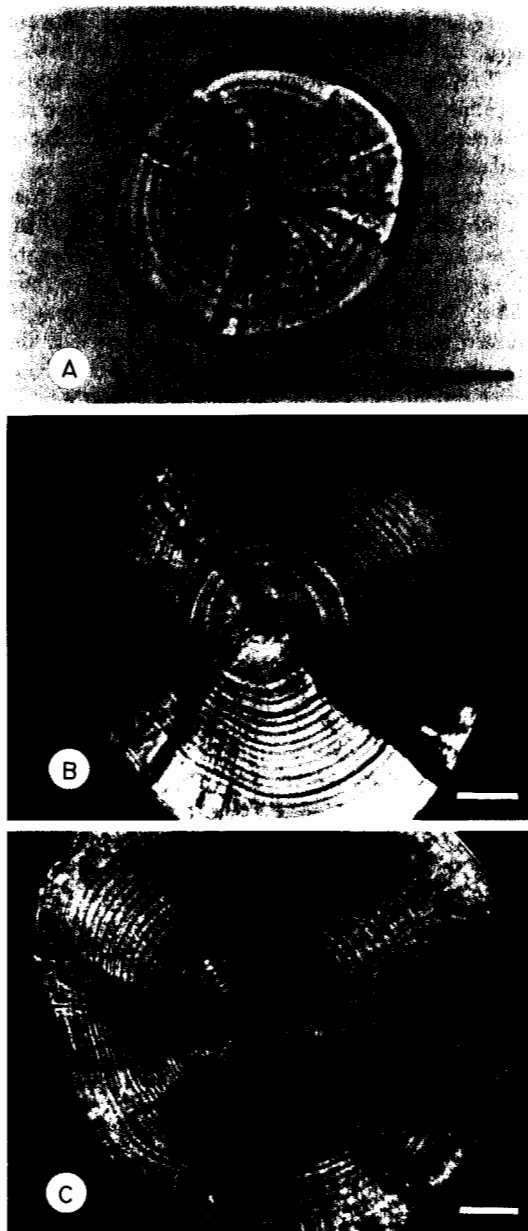


FIGURE 1.—Photomicrographs of whole sagittal otoliths from (A) a 9-d-old, 5.7-mm standard length king mackerel larvae, (B) a 25-d-old, 17.2-mm standard length wild gulf menhaden larva, and (C) a 31-d-old, 18.4-mm standard length laboratory-reared gulf menhaden larva. All bars = 25  $\mu$ m.

these regressions were used as correction factors, and we back-calculated lengths at successive rings using direct proportions. Back-calculated lengths were used to construct half-rank matrices for wild and laboratory-reared gulf menhaden and king mackerel (Tables 1–3). Cells in the matrices for gulf menhaden contain subsets of the data for each observed age and increment number for illustrative purposes; the cells of the matrix for king mackerel contain mean back-calculated lengths for each combination of observed age (d) and increment number. The matrices (Tables 1–3) contain both observed and back-calculated growth information. Observed growth is represented by successive observed mean lengths at age; back-calculated growth is estimated by the successive weighted mean lengths at age.

#### *Size-Selective Mortality*

Coefficients of variation ( $CV = 100 \times SD/\text{mean}$ ) in standard length at age were greater for observed lengths than for back-calculated lengths for both wild and laboratory-reared gulf menhaden, as well as for king mackerel (Table 4), although the difference for laboratory-reared gulf menhaden was very small. Lower average variation in length for back-calculated compared with observed lengths can be explained by size-selective mortality. The back-calculated data contain length-at-age estimates for each previous age of larval life, whereas the observed data comprise only lengths at the ages of capture. Thus, the back-calculated data contain estimates of length at previous ages from a subset of the original population after the population had been subjected to mortality. A reasonable interpretation is that size-selective mortality of the smallest individuals of a given age has biased the size-frequency distribution of the back-calculated sample toward larger, faster-growing larvae, compared with the observed length-at-age sample. That is, the culling of slower-growing larvae reduced the variance in length at age in back-calculated relative to observed data.

There is evidence of size-selective mortality of the smallest larvae at age in the columns of the length-at-age matrix for wild but not for laboratory-reared gulf menhaden. In the ANCOVA used to test for significant trends in the matrix for wild gulf menhaden, the slope was positive, indicating an overall tendency for increasing back-calculated length for older larvae, and observed age was a highly significant effect in the model (Table 5). Surprisingly, evidence for size-selective mortality

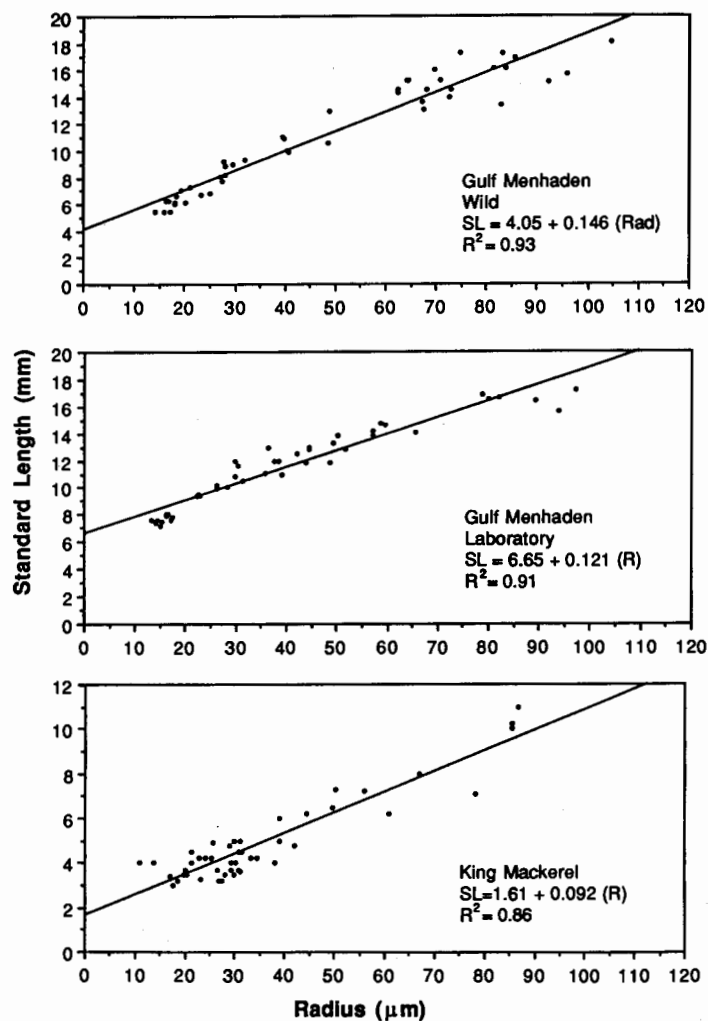


FIGURE 2.—The regressions of standard length (SL) on otolith radius (Rad or R) for wild and laboratory-reared gulf menhaden larvae and king mackerel larvae used to back-calculate lengths for each radius measurement.

TABLE 1.—Half-rank matrices of back-calculated mean standard length (SL) at age (d) for wild gulf menhaden larvae. Only matrix values at 5-d intervals are shown, but weighted means incorporate the complete data set for 47 larvae.

Observed age (d) or statistic	N	Mean observed SL (mm)	Increment number					
			5	10	15	20	25	30
5	4	6.0	6.0					
10	1	8.1	7.0	8.1				
15	1	9.3	7.1	7.9	9.3			
20	1	13.0	7.7	8.8	10.7	13.0		
25	3	16.5	7.6	9.0	11.0	13.6	16.5	
30	1	17.3	7.7	9.3	10.5	12.8	14.1	16.1
Weighted mean			7.0	8.6	10.4	12.6	14.4	15.4
Growth increment				1.6	1.8	2.2	1.8	1.0

TABLE 2.—Half-rank matrices of back-calculated mean standard length (SL) at age (d) for laboratory-reared gulf menhaden larvae. Only matrix values at 5-d intervals are shown, but weighted means incorporate the complete data set for 45 larvae.

Observed age (d) or statistic	N	Mean observed SL (mm)	Increment number					
			5	10	15	20	25	30
7	2	7.1	6.0					
10	1	7.8	6.1	7.3				
14	1	10.0	6.8	8.0				
20	2	12.5	6.4	7.6	10.4	12.5		
24	1	11.9	6.0	7.0	8.5	10.2		
31	1	14.8	6.0	6.9	8.5	10.5	12.2	14.3
Weighted mean			6.1	7.4	8.9	10.6	12.3	14.3
Growth increment				1.3	1.5	1.7	1.7	2.0

of smallest fish at age is not evident in the matrix for wild king mackerel (Table 3). Although there was a slightly positive slope for observed king mackerel age in the ANCOVA model, it was not significant (Table 5). Finally, the columns of the matrix for laboratory-reared gulf menhaden had a slightly negative, but significant, slope, indicating a trend for decreasing back-calculated size for older larvae (Tables 2, 5).

Our results support the widely held idea that larger and faster growing larvae are more likely to survive than smaller and slowly growing larvae, and we wished to elucidate the cause. We hypothesized that predation on the smallest members of a cohort was the agent of size-selective mortality. To evaluate this hypothesis we compared the back-calculated length-to-age matrices for wild and laboratory-reared gulf menhaden (Tables 1, 2), expecting that because laboratory-reared larvae were not exposed to predators their matrix would show no evidence of size-selective mortality. The matrix for wild gulf menhaden did show significant evidence of size-selective mortality of the smaller fish

of a given age, and the matrix of laboratory-reared fish showed a significant trend in the opposite direction (Tables 1, 5). The cause of the small negative slope in laboratory-reared fish is unknown, but we posit that predation was the principal cause of size-selective mortality among wild fish.

The difference in variation in observed versus back-calculated growth of wild and laboratory-reared gulf menhaden may also support predation as the agent of mortality. As stated above, the coefficient of variation in standard length at age was greater for observed than for back-calculated lengths in all three samples. However, the difference in the average error in length at age was much larger for wild than for laboratory-reared gulf menhaden. The coefficient of variation was 11% higher among observed than among back-calculated lengths for wild gulf menhaden and 73% higher for wild king mackerel, but only 2% higher for laboratory-reared gulf menhaden. We suggest that the average differences in the error in length at age were larger for wild fish than for laboratory-reared fish because wild fish were subjected to the

TABLE 3.—Half-rank matrices of back-calculated mean standard lengths (SL, mm) at age (d) for 51 king mackerel larvae.

Observed age (d) or statistic	N	Mean observed SL (mm)	Increment number									
			2	3	4	5	6	7	8	9	10	11
2	1	4.0	4.0									
3	2	3.5	2.7	3.5								
4	5	3.9	2.6	3.2	3.8							
5	8	3.9	2.5	3.0	3.5	4.0						
6	10	4.2	2.2	2.7	3.2	3.7	4.1					
7	7	3.9	2.0	2.4	2.8	3.2	3.6	3.9				
8	8	5.3	2.1	2.6	3.1	3.6	4.0	4.6	5.3			
9	4	6.0	2.2	2.8	3.3	3.9	4.5	5.0	5.5	6.0		
10	2	8.7	2.5	3.1	3.8	4.4	5.0	5.6	6.5	7.8	8.6	
11	4	8.4	2.5	3.0	3.5	3.9	4.5	5.0	5.7	6.3	7.3	8.6
Weighted mean			2.4	2.8	3.3	3.7	4.1	4.7	5.6	6.5	7.7	8.6
Growth increment				0.4	0.5	0.4	0.4	0.6	0.9	0.9	1.2	0.9

TABLE 4.—Means, coefficients of variation (CV =  $100 \times \text{SD}/\text{mean}$ ), and sample sizes ( $N$ ) for larval standard lengths (mm) at age.

Statistic	King mackerel	Wild gulf menhaden	Laboratory-reared gulf menhaden
<b>Observed</b>			
Mean	4.9	11.1	11.5
CV	38.5	11.2	8.5
$N$	51	47	45
<b>Back-calculated</b>			
Mean	3.8	9.3	8.5
CV	22.3	10.1	8.3
$N$	270	804	921

influence of predation that culled the slower-growing larvae.

To investigate these conclusions more fully, we compared least-squares linear regression coefficients of mean back-calculated length on observed age for each column of the matrix for wild and laboratory-reared larvae, reasoning that the slopes were age-specific indices of the intensity of size-selective mortality. There was evidence for size-selective mortality of wild larvae because all slopes were positive (Figure 3); there is no evidence for size-selective mortality of laboratory-reared fish because all slopes were negative. Among wild larvae, size-selective mortality increased quickly to a plateau at 5–7 d, declined gradually to 14 d, and then dropped markedly to its lowest value after 16 d. This pattern suggests that larvae were subjected to predation soon after hatching and may have mostly run the predatory

TABLE 5.—Analysis of covariance (increment number is the covariate) of back-calculated standard lengths at age, testing the significance of size-selective mortality in wild and laboratory-reared gulf menhaden and king mackerel.

Source	df	Slope	F	P
<b>Wild gulf menhaden (<math>R^2 = 0.895</math>)</b>				
Observed age	1	0.04	71.58	<0.0001
Increment number	1	0.32	4,525.37	<0.0001
Error	804			
<b>Laboratory-reared gulf menhaden (<math>R^2 = 0.941</math>)</b>				
Observed age	1	-0.05	317.60	0.0001
Increment number	1	0.33	12,502.61	<0.0001
Error	921			
<b>King mackerel (<math>R^2 = 0.710</math>)</b>				
Observed age	1	0.025	0.87	0.353
Increment number	1	0.56	658.13	<0.001
Error	270			

gauntlet by age 14 d because the intensity of size-selective mortality declined markedly thereafter. However, the data are weak for older ages due to greatly diminished sample sizes; therefore, those slopes should be interpreted with caution.

#### Effects of Size-Selective Mortality on Growth

Regression models of observed and back-calculated growth illustrate the effects of size-selective mortality on growth. The regression calculated from observed length-at-age data in the matrix indicates that wild gulf menhaden grew at a rate of 0.44 mm/d (Table 6). Average growth estimated from the slope of the regression of weighted mean

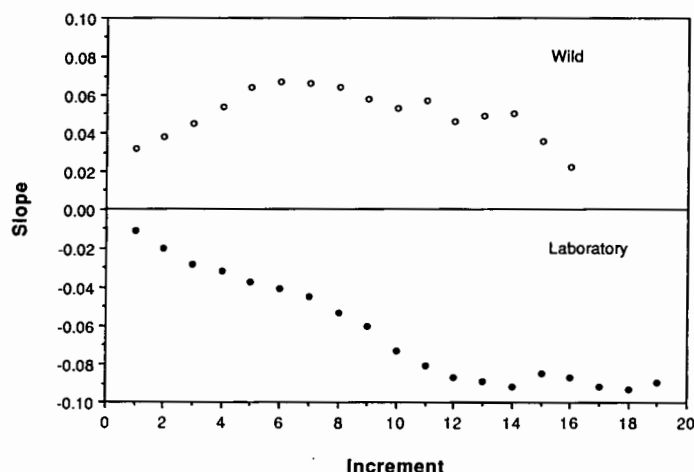


FIGURE 3.—Slopes of least-squares linear regressions of mean back-calculated standard length on age for each column (increment group) plotted on increment number for wild gulf menhaden larvae, showing the magnitudes and time courses of size-selective mortality.

TABLE 6.—Regression (growth) models of observed (A), back-calculated (B), and adjusted back-calculated (C) standard length (SL) for wild and laboratory-reared gulf menhaden and king mackerel.

Model	N	R <sup>2</sup>
<b>Wild gulf menhaden</b>		
(A) SL = 3.45 + 0.44(observed age)	45	0.91
(B) SL = 3.73 + 0.43(increment)	804	0.84
(C) SL = 4.76 + 0.33(increment) + 0.046(observed age)	804	0.89
<b>Laboratory-reared gulf menhaden</b>		
(A) SL = 5.54 + 0.29(observed age)	43	0.90
(B) SL = 4.49 + 0.31(increment)	921	0.92
(C) SL = 5.45 + 0.33(increment) - 0.052(observed age)	921	0.94
<b>King mackerel</b>		
(A) SL = 0.82 + 0.61(observed age)	51	0.54
(B) SL = 1.57 + 0.58(increment)	289	0.71
(C) SL = 1.42 + 0.57(increment) + 0.025(observed age)	270	0.71

back-calculated length at age was 0.43 mm/d. The difference in the slopes of the regressions was significant ( $F = 8.2$ ;  $df = 1, 89$ ;  $P < 0.01$ ;  $R^2 = 0.86$ ) and may have been a result of size-selective mortality. In this case, the slope decreased and the intercept increased because slower-growing fish may have been differentially removed from the population and were increasingly underrepresented at younger ages in back-calculated samples.

To estimate the magnitude of the influence of size-selective mortality on growth and to correct growth for the effect of size-selective mortality, we computed ANCOVAs of back-calculated standard length at age (cells) with increment number (columns) as the main effect and observed age (rows) as the covariate. As pointed out above, slopes of regressions of weighted mean back-calculated lengths at age are estimates of average growth (mm/d). These estimates may have an embedded bias due to size-selective mortality. For example, for wild gulf menhaden, the slope for the main effect from the ANCOVA model provides an unbiased (adjusted) estimate of growth of 0.33 mm/d, which represents a decrease of 25% from observed growth and 23% from back-calculated growth. The observed age (covariate) effect (i.e., the average slope of mean back-calculated standard length on observed age [rows] for each increment [column]) provides an estimate of the bias in average growth attributable to size-selective mortality. We interpret this slope as indicating that for each day increase in age, back-calculated length at age will be biased by the amount of the slope. The covariate indicates that the growth es-

timates for wild gulf menhaden were biased by 0.046 mm/d (Table 6). That is, the average size of 1-d-old larvae will be overestimated by 0.046 mm when back-calculated from 10-d-old fish, as compared with the average size determined from observed length at age for 1-d-old fish. Because there was a trend for decreasing back-calculated size for older larvae in the columns of the length-at-age matrix for laboratory-reared gulf menhaden (Table 2), our growth adjustment analysis increased the growth estimate slightly. Thus, adjusted growth was 6% higher than back-calculated growth and 14% higher than observed growth (Table 6). For king mackerel, adjusted growth was only 7% less than observed growth and 2% less than back-calculated growth (Table 6). However, in light of the ANCOVA for king mackerel, trends in length at age in the matrix were not significant (Table 5).

### Discussion

Several types of back-calculated growth information on gulf menhaden and king mackerel are contained in the half-rank matrices (Tables 1–3): average growth, date- or daily-cohort-specific growth, and time-specific growth. Average growth for the time period equal to the age of the oldest larva used in the analysis (31 d for gulf menhaden and 11 d for king mackerel) plus the length of the sampling period is represented by the successive daily weighted-mean lengths at age. This daily growth is analogous to the annual population growth of Ricker (1975). Average daily growth increments (last row in the tables) are obtained by subtraction of successive weighted means (next to last row in the tables).

The diagonals in the matrices contain time-specific growth information. For example, if the king mackerel larvae in this analysis were collected on 10 September, then growth represented by the uppermost diagonal of length at age (4.0, 3.5, 3.8, 4.0, 4.1, 3.9, . . . mm SL at days 2, 3, 4, 5, 6, 7, . . .) occurred on 10 September. Each lower diagonal of length at age represents growth 1 d earlier. This is equivalent to the annual cohort growth comparisons made on walleye *Stizostedion vitreum* by Weisberg and Frie (1987) and is potentially useful in evaluating the influence of short-term factors (e.g., environmental variability) that may influence growth.

This concept can be applied to the last back-calculated lengths at age (diagonal), which represents growth that occurred over a time interval equal to the sampling interval. For example, if the king mackerel in the sample were collected over



a 5-d sampling period, the absolute growth rate described by 4.0, 3.5, 3.8, 4.0, 4.1, 3.9 . . . mm SL at days 2, 3, 4, 5, 6, 7 . . . represents growth that occurred during that 5-d interval. Ricker (1975) refers to this rate as the true growth rate because it represents growth that occurred under most recent conditions, compared with the population growth rate that is the average growth over the period equal to the oldest age of the fish in the sample plus the duration of the sampling period. Similarly, Methot (1981) and others have used the last few back-calculated lengths at age on larval otoliths to represent recent growth.

Cohort-specific daily growth rate is represented by lengths at age in the rows of the matrix. The cohort is defined as the larvae spawned on one day if all larvae in the sample were collected on a specific day or larvae spawned over a time interval equal to the sampling interval. This aspect of the matrix might allow evaluation of genetic effects on cohort growth, presuming that larvae spawned on different days have different parents. However, size-selective mortality effects, if present, would confound cohort (row) effects.

Results showed lower average variation in length for back-calculated compared with observed length, which can be explained by size-selective mortality. This interpretation of the relative error in back-calculated and observed data is consistent with that of Pepin (1988), who used a stochastic numerical model to simulate the influence of variations in food and size-selective predators on growth and survival of larval fish. He concluded that as predation pressure increases, for any given prey level, the culling of slow-growing larvae by predators results in an apparent increase in growth rate and reduces the variance in growth. In contrast, Bradford and Geen (1987) compared back-calculated and observed length at age for laboratory-reared chinook salmon *Oncorhynchus tshawytscha* and concluded, based upon a higher coefficient of variation for observed lengths, that otolith growth was conservative compared with fish growth and cautioned against using back-calculation to derive growth estimates. The differences Bradford and Geen observed may have been the effect of size-selective mortality. Although selective mortality for the slowest-growing (smallest) larvae of a given age is a reasonable explanation for our results for king mackerel and gulf menhaden larvae, the reverse—that faster-growing (larger) larvae were more vulnerable to mortality—has been shown to sometimes be the case (Lit-

vak and Leggett 1992; Cowan and Houde 1992; Pepin et al. 1992).

Although our results suggest size-selective mortality of gulf menhaden, probably caused by predation, this was not the case for king mackerel, which grow more than twice as fast as gulf menhaden (0.8 mm/d and 0.3 mm/d, respectively; DeVries et al. 1990; Warlen 1988). Exemplifying the large-prey strategy described by Hunter (1981), king mackerel consume other fish larvae almost exclusively (Finucane et al. 1990), which requires them to exert greater searching effort and swim faster. Thus, they are less vulnerable to predation (Bailey and Houde 1989) but have a high metabolic rate and energy requirements. This implies that starvation may be an important cause of mortality for king mackerel, particularly during the first few days after hatching. This conclusion is supported by histological evidence that rates of starvation and malnutrition among preflexion Pacific sierra *Scomberomorus sierra* (Spanish mackerel) off Panama were high (40–50%/d) and that larvae could not survive without feeding beyond 48 h (Margulies 1993). This large-prey strategy may also result in high variability in size, perhaps because individual prey encounter rates and feeding success rates vary greatly (Pepin 1988). For example, the coefficient of variation in observed length at age for king mackerel was 38.5, compared with 11.2 and 8.5 for wild and laboratory-reared gulf menhaden, respectively. Intuitively, this increased variation in size at age should provide the potential for a strong influence of size-selective mortality on growth. Gulf menhaden, the small-prey strategist, were more uniform in length at age; thus, the potential for bias due to size-selective mortality should have been less. However, our results do not support this logic because the matrix showed no significant evidence of size-selective mortality for king mackerel. Pepin (1988) concluded from his numerical simulation of the influence of size-selective predation on growth that when variability in growth rates is high, the effects of size-selective mortality on growth histories are larger and more easily detected than when variability in growth rates are low. However, individual-based simulation modeling suggested that when growth rate and size variation were considered independently, conditions of low growth rate and high variation in size resulted in the greatest change in growth from size-selective mortality (Rice et al. 1993). Our results support the idea that both growth rate and variation in size must be considered to evaluate potential effects of size-

selective mortality. For example, although there was high size variation in king mackerel, the high absolute growth rate did not allow enough time for size-selective mortality to produce a marked effect on growth. However, our findings may also suggest that in the wild, growth rate and variation in size are not independent; that is, high growth rate leads to high size variation and vice versa.

Our results on the influence of size-selective mortality on growth estimates have implications for several aspects of the ecological study of fish larvae. A primary assumption of using observed length-at-age data to represent growth is that all fish in the sample have similar growth and mortality histories. For larval and juvenile fish, as with adult fish (Lee 1912), this is frequently not the case (Rosenburg and Haugen 1982; Post and Prankevicius 1987; Rice et al. 1987). Under the influence of size-selective mortality, as in the case of gulf menhaden, we have shown that growth rate calculated from observed values are as much as 25% higher than corrected growth. Growth comparisons made under known similar conditions of mortality may safely ignore the potential influence of size-selective mortality. However, for growth comparisons when mortality conditions are not likely to be similar, e.g., under the influence of environmental conditions (thermal and riverine fronts, eddies, upwelling, etc.) that affect the distribution of larval fish and their predators, the effects of size-selective mortality on growth may be important.

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